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Deep-sea holothurians (Echinodermata, Holothuroidea) from the Colombian Southern Caribbean Sea

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Abstract
Fifteen morphotypes of deep-sea holothurians were documented by photography or videography at depths of 596–2,566 m, using Remote Operated Vehicles (ROV) video surveys and towed camera transects, during hydrocarbon exploratory activities in the Colombian Southern Caribbean. Most of the morphotypes were identified to the species level based on the images. The species belong to four orders, Apodida (1 species), Persiculida (3 species), Elasipodida (8 species), and Synallactida (3 species). Four species, three genera, and three families are reported for the first time in the Colombian Caribbean Sea. Some of the reports also represent first records for the Caribbean Sea and the Atlantic Ocean.

Keywords
Apodida, Elasipodida, Persiculida, ROV video survey, Synallactida, towed camera, ultra-deep waters.

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Introduction

During hydrocarbon exploratory activities in the Southern Colombian Caribbean, several images of deep-sea cucumbers were acquired through ROV video surveys and towed camera transects. Although specimens were not collected, most of the images show enough detailed taxonomic characteristics to accurately identify families or species, as well as to describe some features of the habitat and report swimming behaviors. Images obtained by ROV and towed camera surveys provide new and valuable information about benthic and bathypelagic megafauna from great depths, which are unexplored not only in the Colombian Caribbean Sea but also in other regions. In recent years, several publications on the deep-sea megafauna from the Colombian Southern Caribbean have provided new records for fishes and invertebrates, including cnidarians and mollusks, among others (Digby et al. 2016; Acero et al. 2018; Guerrero-Kommritz et al. 2018a, 2018b; Cedeño-Posso et al. 2019; Dueñas et al. 2019). Particularly for echinoderms, studies such as in the Gulf of Mexico and around the world have provided *in situ* images of several species, and these images are the basis for new records of species as well as ecological information (Pawson 1982; Miller and Pawson 1990; Bluhm and Gebruk 1999; Gebruk 2008; Rogacheva et al. 2013; Pawson et al. 2015; Stratman et al. 2018; Victorero et al. 2018).

Species diversity of sea cucumbers from the Colombian Caribbean Sea has been characterized for shallow

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to deep-sea environments down to 1,000 m depth (Borrero-Pérez et al. 2003; Benavides-Serrato and Borrero-Pérez 2010). However, deeper bathyal depths (>1000 m), abyssal, and hadal zones are almost unknown. There are some scattered records from cruises in the 1960s and 1970s, such as the R/V John Elliot Pillsbury, Alaminos, and Gyre (Bayer et al. 1970; Borrero-Pérez et al. 2012; Prestridge 2016; Borrero-Pérez et al. 2019). Holothurians previously recorded in Colombia mostly belong to the families Synallactidae and Molpadiidae and have a wide bathymetric distribution starting at depths of 500 m (Borrero-Pérez et al. 2003; Benavides-Serrato and Borrero-Pérez 2010). In this paper, we report bathyal and abyssal holothurians from the Colombian Southern Caribbean Sea. We also include taxonomic and behavioral information obtained through images and videos, increasing the knowledge of biodiversity in deep-sea unexplored areas not only for the Colombian Caribbean but for the wider Caribbean region.

Methods

Hydrocarbon exploratory activities in the Colombian Caribbean usually include ROV video surveys and/or towed camera transects. During exploratory activities between 2015 and 2017, sea cucumbers were sighted in deep Colombian waters below 1500 m in depth. ROV surveys were conducted in 80–100 m-long transects in a cross fashion, north, south, east, and west, from a central point. Towed camera transects were also assessed taking still images every 2–3 seconds for a maximum of 4 hours. Sampling locations are provided in Figure 1. All video footage and still images were analyzed for the presence of sea cucumbers and, when found in the ROV videos, snapshots were taken using the software GOM player and VLC media player. Data obtained from each image was assembled in a Darwin Core standard (DwC) file and is available through the Integrated Publishing Tool of the OBIS and GBIF Colombian nodes (SIBM–SIB Colombia) (https://ipt.biodiversidad.co/sibm/resource?r=anadarko_holothuroidea) (Puentes et al. 2019a). For every species in this paper, data collection of each image is presented in material examined section including the identification (ID) of each record in Puentes et al. (2019a).

Species identifications were made on the basis of diagnostic external characters observed in the images. The equipment used for image acquisition (ROV and

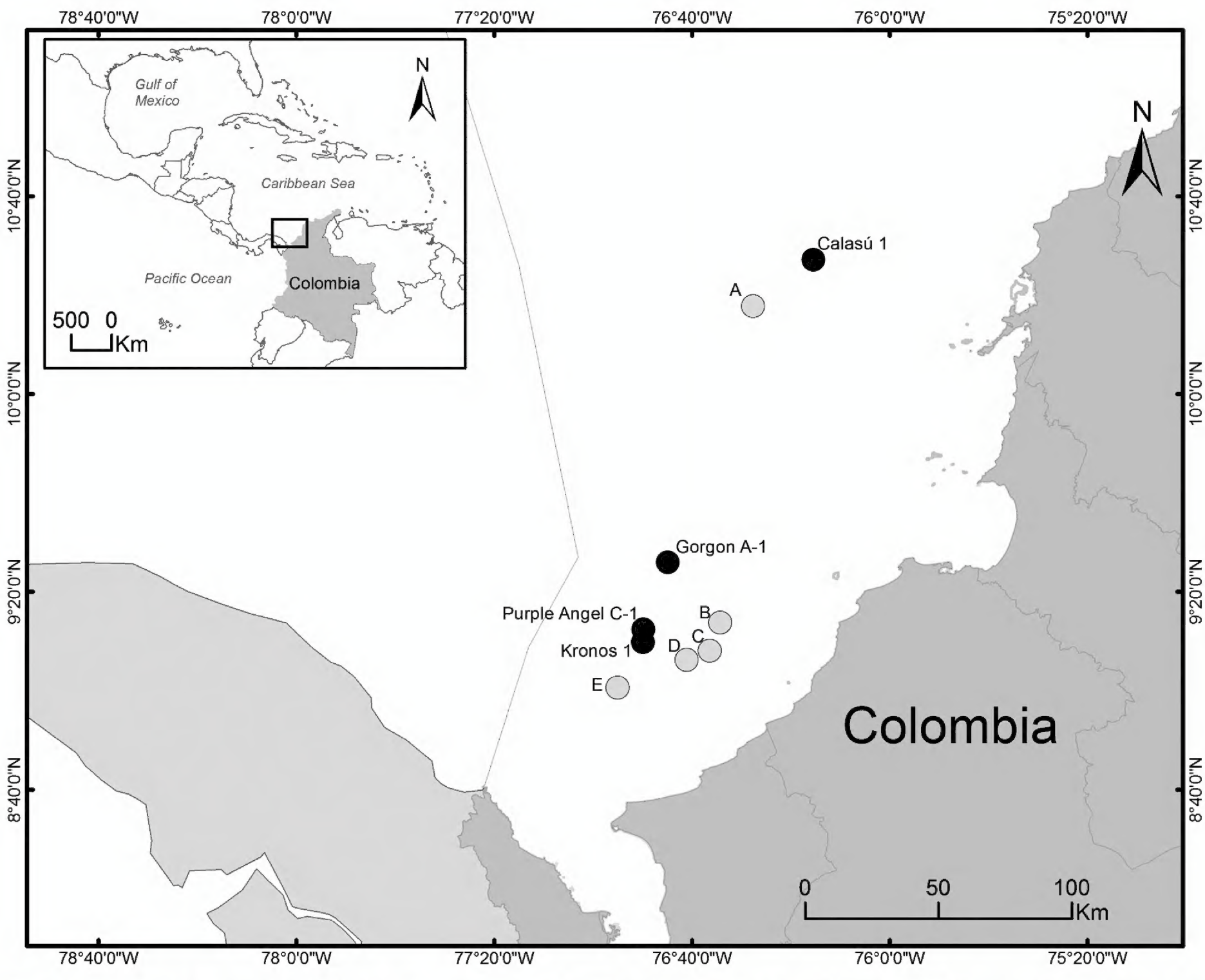

Figure 1. Geographical location of holothurian occurrences at the Colombian Southern Caribbean Sea. Black circles depict the wells that were drilled and gray circles correspond to other surveyed areas. Coordinates of the study area: 09.27°N–10.369° N, 076.481°W–076.932°W.

towed camera) had no laser scales; hence, there is no size reference for any of the images analyzed. In order to provide all the taxonomic characteristics of each species, the identification section includes not only the diagnostic external characters observed on the images but also internal or other external structures that were not observed. In the comments section, we extend the discussion on the characters that were observed in the images.

Results

ROV video surveys and towed camera transects provided images of 15 morphotypes of deep-sea holothurians from the Colombian Southern Caribbean. They belong to four orders: Apodida (1 morphotype), Persiculida (3), Elasipodida (8), and Synallactida (3). Ten morphotypes were identified to species, although three of them were not confirmed (they are presented as cf.). Additionally, four morphotypes were identified only to genus level, *Pseudostichopus* Théel, 1886, *Laetmogone* Théel, 1879, *Peniagone* Théel, 1882, and *Synallactes* Ludwig, 1894; however, the last two were not confirmed. Finally, one specimen was identified to family level (Synallactidae sp.) (Table 1). Three families, four genera, and four species are reported for the first time in the Colombian Caribbean Sea; some of them also represent first records for the whole Caribbean Sea and the Atlantic Ocean (Table 1).

Class Holothuroidea
Order Apodida Brandt, 1835
Family Chiridotidae Östergren, 1898
Genus *Chiridota* Eschscholtz, 1829

***Chiridota heheva* Pawson & Vance, 2004**
Figure 2A, B

Material examined. COLOMBIA • 1; Southwestern Caribbean, Calasú 1; 10.476°N, 076.247°W; depth 2394 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L08:3436 • 3; Southwestern Caribbean, Calasú 1; 10.381° N, 076.326°W; depth 2403 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L10:2657.

Identification (after Pawson and Vance 2004). Live colour is blue to bluish-purple, with numerous conspicuous whitish spots (wheel papillae) in all interradii. Tentacles with terminal discs carrying approximately 20 discrete, finger-like digits, which are free and extended during feeding. Tentacles equally spaces; no ventral gap. Inhabitant of bathyal/abyssal cold seeps and anthropogenic habitats.

Table 1. Check list of the deep-sea holothurians from the Southern Colombian Caribbean recorded in the present study.

Taxa	Depth (m), present study	Depth (m), from literature	First record from Colombia
Class Holothuroidea			
Order Apodida			
Family Chiridotidae			
Chiridota heheva Pawson & Vance, 2004	2394	2178–3998	X (1)
Order Persiculida			
Benthothuria funebris Perrier R., 1898	1563–2297	782–4636	X (2)
Family Gephyrothuriidae			
Paroriza pallens (Koehler, 1896)	1803–1809	794–5000	X (2)
Family Pseudostichopodidae			
Pseudostichopus sp.	596–2259	—	
Order Elasipodida			
Family Elpidiidae			X (1)
? *Peniagone* sp.	1794–2487	—	? X (1)
Family Laetmogonidae			X (3)
Psychronaetes hanseni Pawson, 1983	1804–2087	4800–5200	X (4)
Laetmogone sp.	1806	—	X (3)
Family Pelagothuriidae			
Enypniastes eximia Théel, 1882	1575–2562	516–5689	
Family Psychropotidae			
Benthodytes cf. *abyssicola* Théel, 1882	1850–2487		? X (1)
Benthodytes cf. *sanguinolenta* Théel, 1882	2307	768–7250	
Benthodytes cf. *typica* Théel, 1882	2076–2565	1400–3514	2nd
Psychropotes depressa (Théel, 1882)	1182–2566	957–4200	2nd
Order Synallactida			
Family Synallactidae Ludwig, 1894			
? *Synallactes* sp.	651	—	? X
Synallactidae sp.	2236–2564	—	
Family Deimatidae			
Deima validum validum Théel, 1879	1986	724–5424	2nd

In the last column: "X" indicates first record from Colombia and numbers in parentheses: (1) first record from the Caribbean Sea; (2) first record for genus and species from the Caribbean Sea; (3) first record from the Tropical and Southwestern Atlantic; (4) first record from the Atlantic Ocean; 2nd indicates the second record from Colombian Caribbean Sea.

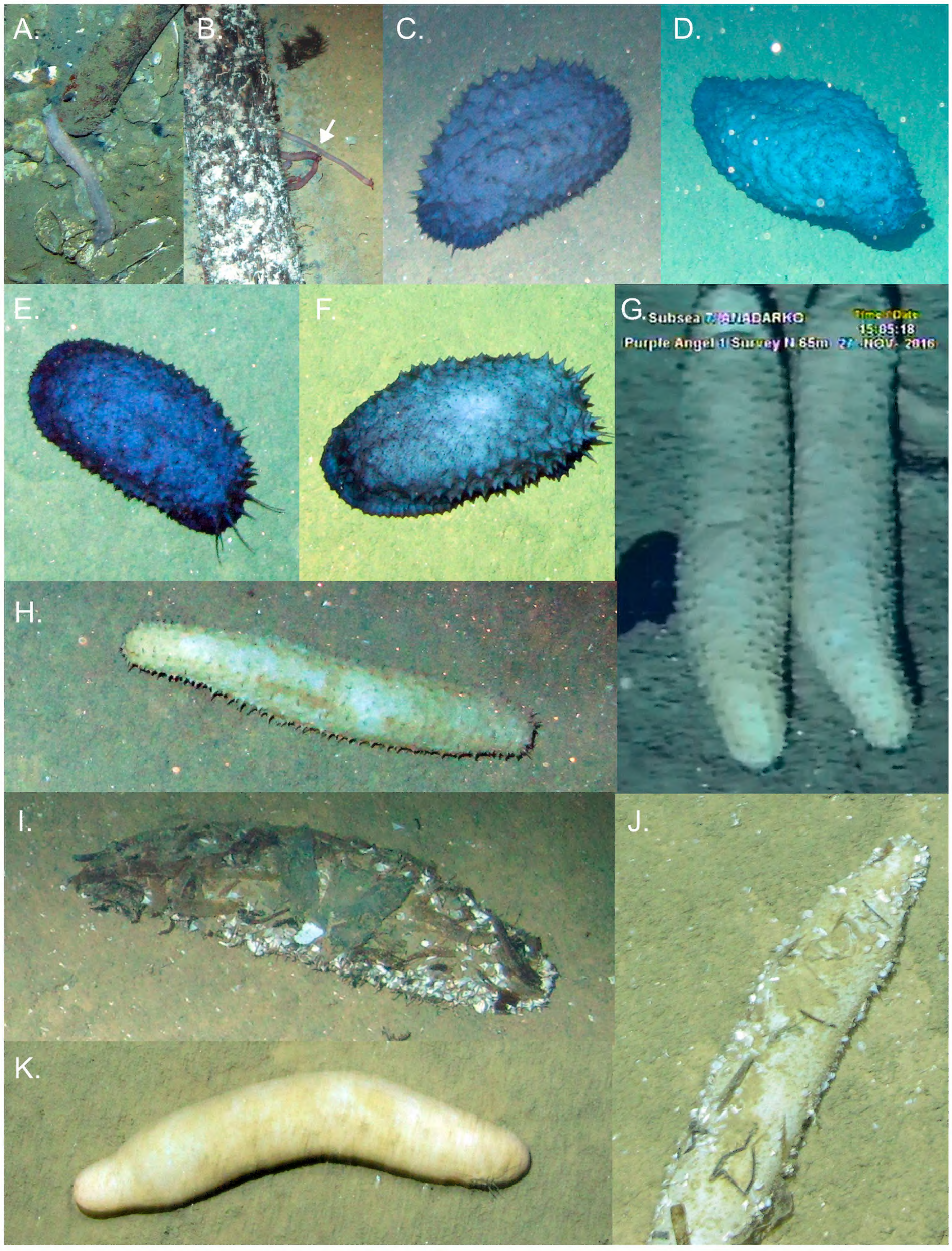

Figure 2. Towed-camera *in situ* images of deep-sea holothurians from the Colombian Southern Caribbean. **A, B.** *Chiridota heheva*, arrow indicate three specimens. **C–F.** *Benthothuria funebris*. **G, H.** *Paroriza pallens* (**G**: ROV images). **I–K.** *Pseudostichopus* spp.

Distribution. This is the first record for the Colombian Caribbean Sea and the southern Caribbean Sea. Previously, *C. heheva* was reported from cold seeps in the eastern Gulf of Mexico (Florida), the shipwreck *Central America* on the eastern coast of the USA (Savannah, Georgia), and wood blocks near Puerto Rico; the reported depth range was from 2,178–3,998 m (Pawson and Vance 2004).

Comments. Because the identifications are based only on images, it was not possible to review every diagnostic character; however, the colour in life (purplish or bluish) and the conspicuous whitish spots (wheel papillae) in all interradii allowed us to confirm the species. Pawson and Vance (2004) compared *C. heheva* with other two *Chiridota* abyssal species. *Chiridota hydrothermica* Smirnov & Gebruk, 2000 from hydrothermal vents in West and Southeastern Pacific differs in colour, being semi-transparent, grey-brownish with the wheel papillae coloured the same as the body and therefore not conspicuous (Smirnov et al. 2000). *Chiridota laevis* (O. Fabricius, 1780) from the North Atlantic and North Pacific also differs in colour, being pinkish, pinkish brown, greyish, or yellowish. Van Dover et al. (2013) found *C. heheva* at the Blake Ridge (Savannah, Georgia) in association with the methane seep-associated mussel *Bathymodiolus heckerae* Turner, Gustafson, Lutz & Vrijenhoek, 1998. One specimen recorded in the Colombian Southern Caribbean appears to be associated with *Bathymodiolus* sp. in a chemosynthetic community, and the other three specimens were associated with a log of wood.

Order Persiculida Miller, Kerr, Paulay, Reich, Wilson, Carvajal & Rouse, 2017
Genus *Benthothuria* Perrier R., 1898

***Benthothuria funebris* Perrier R., 1898**
Figure 2C–F

Material examined. COLOMBIA • 1; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1627 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2541 • 1; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1631 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2550 • 1; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1633 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2555 • 1; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1640 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2556 • 2; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1639 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2561• 1; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1641 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2565 • 1; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1641 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2566 • 1; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1641 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2567 • 1; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1641 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2575 • 2; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1642 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2576 • 1; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1656 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2579 • 1; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1662 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2582 • 1; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1690 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2587 • 1; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1697 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2588 • 1; Southwestern Caribbean, Calasú 1; 10.459°N, 076.236°W; depth 2228 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L06:2936 • 1; Southwestern Caribbean, Gorgon A-1; 09.433°N, 076.748°W; depth 2297 m; 26 Feb. 2017; ROV, Moving Image; ACC:ROV-2017-GorgonArr:0022 • 1; Southwestern Caribbean, Purple Angel C-1; 09.209°N, 076.832°W; depth 1819 m; 24 Feb. 2017; ROV, Moving Image; ACC:ROV-2017-NPADep:0023 • 1; Southwestern Caribbean, Purple Angel C-1; 09.207°N, 076.832°W; depth 1808 m; 24 Feb. 2017; ROV, Moving Image; ACC:ROV-2017-OPADep:024(1) • 1; Southwestern Caribbean, Kronos 1; 09.165°N, 076.832°W; depth 1563 m; 27 Aug. 2015; ROV, Moving Image; ROV-VIDEO_TS.IFO_001625979 • 1; Southwestern Caribbean, Kronos 1; 09.165°N, 076.832°W; depth 1562 m; 27 Aug. 2015; ROV, Moving Image; ROV-VTS_01_2.VOB_000061110 • 1; Southwestern Caribbean, Purple Angel C-1; 09.207°N, 076.832°W; depth 1806 m; 24 Feb. 2017; ROV, Moving Image; ROV-VTS_01_0.IFO_001395071 • 1; Southwestern Caribbean, Purple Angel C-1; 09.209°N, 076.832°W; depth 1816 m; 24 Feb. 2017; ROV, Moving Image; ROV-VTS_01_0.IFO_000646120.

Identification (after Heding 1940; Solís-Marín 2003; Pawson et al. 2015). Body elongated, but semispheric in lateral view. Flat ventral sole, limited by a continuous row of papillae. Ventral mouth, and 20 short, dendritic tentacles. Scattered dorsal projections, not confined to radii, and a conspicuous mid-dorsal groove. Colour light purplish (lilac) dorsally, slightly darker ventrally, especially around the margin. No large ambulacral papillae on the dorsal side. Longitudinal muscles are unpaired. One polian vesicle. No ossicles are found in any part of the body wall, tentacles or internal organs.

Distribution. The present record is the first for the genus and the species in the Colombian Caribbean Sea and the Caribbean in general. The species had been recorded from the North Atlantic and from off North Central Gulf of Mexico, North-West Africa and southwestern Greenland, Tanzania, and from the southern Indian Ocean (as *B. valdiviae*; Heding 1940). The depth range has been reported between 782 and 4,636 m (Gage et al. 1985; Rogacheva et al. 2013; Pawson et al. 2015).

Comments. The genus *Benthothuria* comprises three nominal species: *B. cristata* Koehler & Vaney, 1905 and *B. distorta* Koehler & Vaney, 1905, both only known from their type localities at the Indian Ocean, and *B. fusiformis* (Sluiter, 1901) from the North Pacific Ocean

and Indonesia. Currently, a fifth species *B. valdiviae* Heding, 1940 is accepted as *B. funebris*, which is a synonymy suggested in several papers, but with some reservations (Heding 1940; WoRMS 2019a). These species differ in the number of polian vesicles and the presence (*B. valdiviae*) or absence (*B. funebris*) of large papillae along the dorsal ambulacra (Solís-Marín 2003; Pawson et al. 2015). In the Colombian Southern Caribbean Sea specimens with or without large papillae on the anterior part of the body were observed (Fig. 2C–F). *Benthothuria* was formerly assigned to the family Gephyrothuriidae, and after revision, it was referred to the family Synallactidae. However, in the recent proposal of Holothuroidea classification, there is no assigned family for the genus (Miller et al. 2017). All the specimens observed in the Colombian Southern Caribbean were resting on the seafloor, although previous records have documented this species' swimming ability (Rogacheva et al. 2013; Pawson et al. 2015).

Family Gephyrothuriidae Koehler & Vaney, 1905
Genus *Paroriza* Hérouard, 1902

***Paroriza pallens* (Koehler, 1896)**
Figure 2G, H

Material examined. COLOMBIA • 2; Southwestern Caribbean, Purple Angel C-1; 09.207°N, 076.832°W; depth 1809 m; 27 Nov. 2016; ROV, Moving Image; ACC: ROV-2015-Capture_001(1) • 1; Southwestern Caribbean, Kronos 1; 09.219°N, 076.834°W; depth 1809 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015--L17:2480 • 1; Southwestern Caribbean, Purple Angel C-1; 09.207°N, 076.832°W; depth 1803 m; 26 Nov. 2016; ROV, Moving Image; VTS_01_0.IFO_001427760 • 2; Southwestern Caribbean, Purple Angel C-1; 09.207°N, 076.832°W; depth 1805 m; 26 Nov. 2016; ROV, Moving Image; VTS_01_0.IFO_001794480.

Identification (after Solís-Marín 2003; Pawson et al. 2015). Body fusiform, cylindrical, covered with evenly distributed dorsal papillae/tube feet, all subequal in size. Tentacles 20. Colour in life variegated in light yellow. Ossicles are completely lacking in the body wall as in the ambulacral appendices and tentacles Usually, individuals are not covered with detritus.

Distribution. This is the first record for both genus and species in the Caribbean region. *Paroriza pallens* occurs in the northeastern Atlantic from northeastern Spain to the Porcupine Seabight; western Atlantic at the Bahamas and the Gulf of Mexico. It has also been reported in the northern Pacific Ocean and the Philippines Trench (Pawson et al. 2015). The depth range in the Atlantic Ocean is 794–2,100 m and in the Pacific it is known from a depth of 5,000 m (Pawson et al. 2015).

Comments. Currently, four species of *Paroriza* are recognized (WoRMS 2019b). Pawson et al. (2015) proposed a fifth undescribed species from the Gulf of Mexico (*Paroriza*? n. sp.). *Paroriza verrucosa* Massin, 1987, an upper bathyal species from Indonesia, can be distinguished because it has 16 tentacles. *Paroriza grevei* Hansen, 1956 inhabiting hadal depths in Indonesia, and *P. prouhoi* Hérouard, 1902 from abyssal depths in the northern Atlantic and Pacific oceans, differ from *P. pallens* in having the body mostly covered dorsally by papillae/tube feet of varying size (Solís-Marín 2003; Pawson et al. 2015). Two images acquired in the Colombian Southern Caribbean showed paired individuals (Fig. 2G). Aggregations, in pairs or triplets, have been recorded for deep-sea echinoderm species (Pawson 1976), and specifically for *Paroriza pallens*. The purpose of aggregations is for reproduction, although *P. pallens* is hermaphroditic (Tyler et al. 1992).

Family Pseudostichopodidae Miller, Kerr, Paulay, Reich, Wilson, Carvajal & Rouse, 2017

Genus *Pseudostichopus* Théel, 1886

***Pseudostichopus* sp.**
Figure 2I–K

Material examined. COLOMBIA • 1; Southwestern Caribbean, Calasú 1; 10.471°N, 076.235°W; depth 2259 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L02:2286 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 2096 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2385 • 1; Southwestern Caribbean, Kronos 1; 09.219°N, 076.834°W; depth 1804 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L17:2487 • 1; Southwestern Caribbean, Kronos 1; 09.219°N, 076.834°W; depth 1794 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L17:2530 • 1; Southwestern Caribbean, Kronos 1; 09.199°N, 076.819°W; depth 1729 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L18:2605 • 1; Southwestern Caribbean, B; 09.23°N, 076.571°W; depth 596 m; 5 Oct. 2015; towed camera, still image; ACC:TC-2015-L24:2613 • 1; Southwestern Caribbean, Purple Angel C-1; 09.207°N, 076.832°W; depth 1805 m; 27 Nov. 2017; ROV, Moving Image; VTS_01_0.IFO_001758000.

Comments. The specimens observed in the Colombian Southern Caribbean belong to the genus *Pseudostichopus*; however, at least one of them may belong to a different species. The body is more or less cylindrical, slightly tapering and rounded at the extremities. The ventral surface is more or less flat. Colour in life is dirty white to light brown. One of the specimens (Fig. 2I) has the dorsal surface completely covered with what looks like dead seagrass leaves, and thick particles that appear to be pieces of shells. Although the other specimens are partially uncovered, pieces of the same coating remain (Fig. 2J). All these specimens were observed at depths between 1,729 and 2,259 m. One specimen, which was completely uncovered and observed at 596 m depth, could belong to a different *Pseudostichopus* species (Fig. 2K). Currently, 12 species are recognized in the genus *Pseudostichopus* (WoRMS 2019c). Although *Pseudostichopus peripatus* (Sluiter, 1901) and *P. occultatus*

(Marenzeller, 1893) are recorded for the Caribbean Sea, only the last one has been recorded in Colombia (Borrero-Pérez et al. 2012).

Order Elasipodida Théel, 1882
Family Elpidiidae Théel, 1882
Genus *Peniagone* Théel, 1882

? *Peniagone* sp.
Figure 3A–C

Material examined. COLOMBIA • 1; Southwestern Caribbean, Kronos 1; 09.219°N, 076.834°W; depth 1858 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L17:2384 • 1; Southwestern Caribbean, Calasú 1; 10.377°N, 076.31°W; depth 2224 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L12:2399 • 1; Southwestern Caribbean, Calasú 1; 10.377°N, 076.31°W; depth 2330 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L12:2414 • 2; Southwestern Caribbean, Kronos 1; 09.219°N, 076.834°W; depth 1845 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L17:2416 • 1; Southwestern Caribbean, Kronos 1; 09.219°N, 076.834°W; depth 1844 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L17:2419 • 1; Southwestern Caribbean, A; 10.296°N, 076.461°W; depth 2487 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L13:2462 • 2; Southwestern Caribbean, Calasú 1; 10.377°N, 076.31°W; depth 2436 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L12:2486 • 1; Southwestern Caribbean, Calasú 1; 10.377°N, 076.31°W; depth 2235 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L12:2490 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 2055 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2504 • 1; Southwestern Caribbean, Kronos 1; 09.219°N, 076.834°W; depth 1795 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L17:2517 • 1; Southwestern Caribbean, Kronos 1; 09.219°N, 076.834°W; depth 1794 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L17:2525 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 2042 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2544 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 2040 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2550 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 2040 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2551 • 1; Southwestern Caribbean, Calasú 1; 10.38°N, 076.319°W; depth 2348 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L09:2556 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 1978 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2634 • 1; Southwestern Caribbean, Calasú 1; 10.381°N, 076.326°W; depth 2370 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L10:2777 • 1; Southwestern Caribbean, Calasú 1; 10.381°N, 076.326°W; depth 2369 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L10:2783.

Comments. The specimens observed in the Colombian Southern Caribbean belong to the same species probably in the genus *Peniagone* of the family Elpidiidae. The external morphology of the specimens is similar to other elpidiid genera, such as *Peniagone* Théel, 1882 and *Amperima* Pawson, 1965 with swimming representatives. The external characters include: anterior end with a lobe composed of tentacles on the ventral side, and a velum on the dorsal side, and posterior end showing a swimming lobe comprising of crowded tube feet (Rogacheva et al. 2012). The specimens may belong to *Peniagone*, because they are brightly coloured and also have small velum. However, it is not possible to confirm this identification because their ossicles are not visible; ossicles are sometimes visible at high-resolution images or those taken closer (comm. pers. Kremenetskaia A. 2019). Rogacheva et al. (2012) reported *Peniagone*, and other genera of Elpidiidae, such as *Amperima* and *Ellipinion* Hérouard, 1923 as frequent swimmers, meaning they often swim, but spend most of the time on the seafloor; benthopelagic holothurians usually land at the bottom to feed and then take off. Most of our images showed the specimens on the seafloor with tentacles extended for feeding. Elpidiids are very common in the deep sea at lower bathyal and especially abyssal depths; and *Peniagone* is the most species-rich genus in the family, showing the highest diversity of external morphological features (Rogacheva et al. 2013). Currently, 32 valid species are recognized (WoRMS 2019d). In spite of its high diversity at deep environments, the present record of the family is the first in the Caribbean Sea. For the Gulf of Mexico, there are several records of the elpidid *Peniagone azorica* Marenzeller von, 1892 available through the databases GBIF and OBIS (Deep-sea OBIS node 2018). The single record of the family presented by Alvarado and Solís-Marín (2013) corresponds to *Peniagone purpurea* (Théel, 1882) from the Canary Islands in the Eastern Atlantic Ocean.

Family Laetmogonidae Ekman, 1926
Genus *Psychronaetes* Pawson, 1983

***Psychronaetes hanseni* Pawson, 1983**
Figure 3D

Material examined. COLOMBIA • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 2087 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2431 • 1; Southwestern Caribbean, Kronos 1; 09.219°N, 076.834°W; depth 1804 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L17:2490 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 1988 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2618.

Identification (after Pawson 1983). Body fusiform, up to 30 cm long, with pronounced anterior ‘’head” region with large, irregular sized fringe of dorsal papillae. Midventral radius naked, lateral ventral radii each with approximately 15 triangular tubefeet. Dorsal radii each with approximately 30 papillae. Dorsal papillae forming

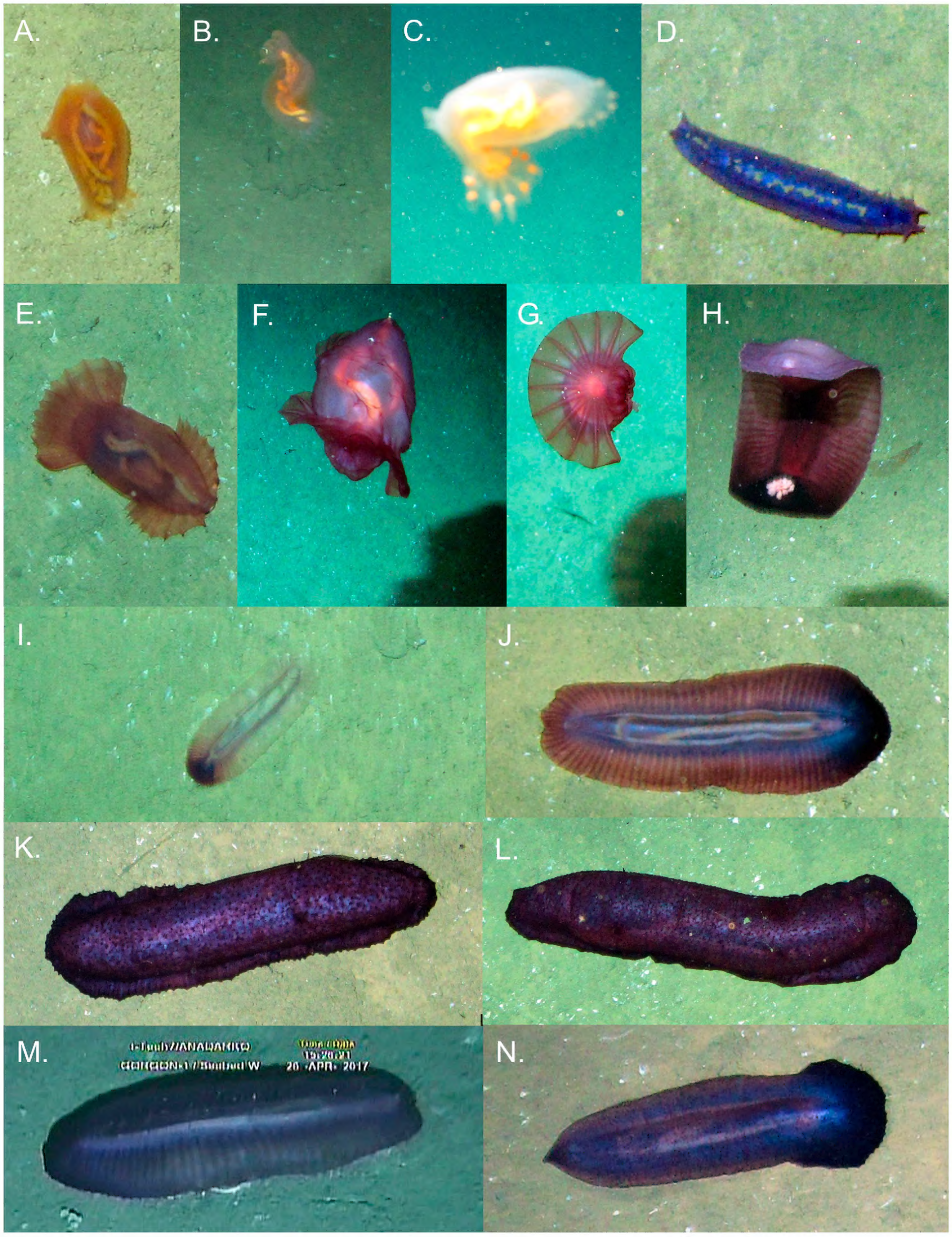

Figure 3. Towed-camera *in situ* images of deep-sea holothurians from the Colombian Southern Caribbean. **A–C.** ?*Peniagone* sp. **D.** *Psychronaetes hanseni*. **E–G.** *Enypniastes eximia*. **H–J.** *Benthodytes* cf. *typica*. **K–L.** *Benthodytes* cf. *abyssicola*. **M.** *Benthodytes* cf. *sanguinolenta*. **N.** Synallactidae sp.

an irregular fringe around the anterior dorsal end of the body. Fifteen tentacles, no circumoral papillae. Ossicles in bodywall wheels of one type, usually 50–60 μm in diameter, usually with 9–12 spokes.

Distribution. The present record is the first for the family for the tropical and southwestern Atlantic, and for the genus and the species for the Atlantic Ocean. *Psychronaetes hanseni* had been recorded only from the eastern

central Pacific (Pawson 1983). The previously reported depth range was 4,800–5,200 m (Pawson 1983); the new record from the Colombian Southern Caribbean extends the depth range to shallower waters up to 1,804 m.

Comments. *Psychronaetes hanseni* is the only species in this genus, and no visible characteristic suggested that the observed specimens belong to a new species. The specimens from the Colombian Southern Caribbean extend greatly the geographical distribution of the species from the Pacific to the Atlantic Ocean (comm. pers. D. Pawson 2019), which could be expected considering that numerous deep-sea holothuroid genera are cosmopolitan (Hansen 1975). The characteristic shape of this species allowed us to identify it from the available images. However, other reports based on better images and if is possible collected specimens would be useful to confirm its distribution in the Atlantic Ocean.

Genus *Laetmogone* Théel, 1879

***Laetmogone* sp.**
Figure 4H

Material examined. COLOMBIA • 2; Southwestern Caribbean, Purple Angel C-1; 09.207°N, 076.832°W; depth 1806 m; 27 Nov. 2016; ROV, Moving Image; ACC:ROV-2016-VTS_01_0.IFO_000186160.

Comments. This specimen belongs to the genus *Laetmogone*. However, it was impossible to identify the genus and species. The body is cylindrical, light pink, and with large and extended tentacles and papillae mostly on the lateral side of the body. This is one of the most diagnostic characteristics in the external morphology of this genus; Théel (1879: 9–10) described it with "back highly convex, ventral surface slightly so; mouth anterior, terminal, subventral; the lateral ambulacra of the trivium with large, not retractile, only a little contractile pedicels, disposed in a single row all along each side of the ventral surface; the odd ambulacrum naked; bivium with highly elongated, flexible, cylindrical, not retractile processes, disposed in a single row all along each of its ambulacra". The specimen was observed at a depth of 1806 m. Currently, 12 species are recognized in the genus *Laetmogone* (WoRMS 2020); the present record is the first for the genus for the tropical and southwestern Atlantic.

Family Pelagothuriidae Ludwig, 1893
Genus *Enypniastes* Théel, 1882

***Enypniastes eximia* Théel, 1882**
Figure 3E–G

Material examined. COLOMBIA • 1; Southwestern Caribbean, Calasú 1; 10.377°N, 076.31°W; depth 2221 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015--L12:2388 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 2065 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2493 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 2044 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2542 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 2042 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015--L16:2545 • 1; Southwestern Caribbean, Calasú 1; 10.38°N, 076.319°W; depth 2342 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L09:2589 • 1; Southwestern Caribbean, Calasú 1; 10.381°N, 076.326°W; depth 2375 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L10:2725 • 1; Southwestern Caribbean, Calasú 1; 10.466°N, 076.242°W; depth 2275 m; 30 Sep. 2015; towed camera, still image; ACC:TC-2015-L05:2733 • 1; Southwestern Caribbean, A; 10.281°N, 076.445°W; depth 2562 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L14:2737 • 1; Southwestern Caribbean, Calasú 1; 10.469°N, 076.25°W; depth 2347 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L07:3219 • 2; Southwestern Caribbean, Calasú 1; 10.469°N, 076.25°W; depth 2355 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L07:3235 • 1; Southwestern Caribbean, Calasú 1; 10.469°N, 076.25°W; depth 2361 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015--L07:3249 • 1; Southwestern Caribbean, Calasú 1; 10.469°N, 076.25°W; depth 2364 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L07:3253 • 1; Southwestern Caribbean, Calasú 1; 10.469°N, 076.25°W; depth 2369 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L07:3269 • 1; Southwestern Caribbean, Calasú 1; 10.453°N, 076.257°W; depth 2207 m; 24 Feb. 2015; ROV, Moving Image; ACC: ROV-2015-VTS_03_1. VOB_000571760 • 1; Southwestern Caribbean, Calasú 1; 10.453°N, 076.257°W; depth 2209 m; 24 Feb. 2015; ROV, Moving Image; ACC: ROV-2015-VTS_04_1. VOB_000354514 • 1; Southwestern Caribbean, Calasú 1; 10.453°N, 076.257°W; depth 2213 m; 3 Mar. 2015; ROV, Moving Image; ACC: ROV-2015-VTS_05_1. VOB_000367486 • 1; Southwestern Caribbean, Purple Angel C-1; 09.209°N, 076.832°W; depth 1822 m; 2 Dic. 2016; ROV, Moving Image; ACC: ROV-2015-Purple Angel 1a Seabed Survey Arrival Dec 2nd 2016 • 1; Southwestern Caribbean, Purple Angel C-1; 09.209°N, 076.832°W; depth 1817 m; 26 Feb. 2017; ROV, Moving Image; ACC: ROV-2015-VTS_01_0.IFO_000587560 • 1; Southwestern Caribbean, Purple Angel C-1; 09.209°N, 076.832°W; depth 1818 m; 27 Feb. 2017; ROV, Moving Image; ACC: ROV-2015-VTS_01_0.IFO_001343160 • 1; Southwestern Caribbean, Gorgon A-1; 09.433°N, 076.748°W; depth 2297 m; 23 Nov. 2016; ROV, Moving Image; ACC: ROV-2015-VTS_01_0.IFO_001452133.

Identification (after Miller and Pawson 1990). Bulbous barrel-shaped body up to 25 cm long, and large anterior webbed veil incorporating up to 12 conical podia. Twenty tentacles around the mouth. Two posterolateral veils each composed of 10–15 webbed podia. Ossicles absent.

Distribution. Cosmopolitan, but most commonly found near continental margins; depth range from 516 to 5,689 m (Miller and Pawson 1990); in the tropical Western

Atlantic, it has been reported only in the Gulf of Mexico and Colombia (Borrero-Pérez et al. 2003; Alvarado and Solís-Marín 2013; Pawson et al. 2015). This is the second record of this species in Colombia and the Southern Caribbean Sea, and it is interesting that the species was common during samplings.

Comments. This benthopelagic species is a well-known swimming sea cucumber species, and its swimming movements have been analyzed by Ohta (1985) and Miller and Pawson (1990). Rogacheva et al. (2012) reported this species as preferential swimmers, meaning that it spends most of time in the water column, landing for feeding. Most of our images show *E. eximia* on the seafloor, with tentacles and its anterior and posterolateral veils extended (Fig. 3E–G).

Family Psychropotidae Théel, 1882
Genus *Benthodytes* Théel, 1882

***Benthodytes* cf. *abyssicola* Théel, 1882**
Figure 3K, L

Material examined. COLOMBIA • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 2094 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2392 • 1; Southwestern Caribbean, Kronos 1; 09.219°N, 076.834°W; depth 1850 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L17:2405 • 1; Southwestern Caribbean, A; 10.296°N, 076.461°W; depth 2487 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L13:2407 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 2089 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2418 • 1; Southwestern Caribbean, A; 10.296°N, 076.461°W; depth 2485 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L13:2470 • 1; Southwestern Caribbean, A; 10.296°N, 076.461°W; depth 2486 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L13:2475 • 1; Southwestern Caribbean, Calasú 1; 10.467°N, 076.242°W; depth 2280 m; 30 Sep. 2015; towed camera, still image; ACC:TC-2015-L03:2480 • 1; Southwestern Caribbean, Calasú 1; 10.467°N, 076.242°W; depth 2289 m; 30 Sep. 2015; towed camera, still image; ACC:TC-2015-L03:2492 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 1998 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2608 • 1; Southwestern Caribbean, Calasú 1; 10.381°N, 076.326°W; depth 2369 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L10:2793 • 1; Southwestern Caribbean, Calasú 1; 10.392°N, 076.325°W; depth 2425 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L11:2961 • 2; Southwestern Caribbean, Calasú 1; 10.459°N, 076.236°W; depth 2299 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L06:3145 • 1; Southwestern Caribbean, Calasú 1; 10.469°N, 076.25°W; depth 2341 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L07:3207 • 1; Southwestern Caribbean, Calasú 1; 10.469°N, 076.25°W; depth 2344 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L07:3012 • 1; Southwestern Caribbean, Calasú 1; 10.469°N, 076.25°W; depth 2369 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L07:3267.

Identification (after Rogacheva et al. 2009). Body elongate, maximum body width at the middle of body. Brim narrow, retractile. Fifteen tentacles; circum-oral papillae present. Dorsal papillae arranged in 2 rows: 3 or 4 pairs of large papillae and 1–5 pairs of minute papillae anterior to the first pair of large papillae or between larger ones; sometimes minute unpaired papillae present. Large papillae evenly distributed along dorsum: first pair located on the anterior third of dorsum; second pair situated close to middle of the dorsum, third pair on posterior third quarter or posterior one-third of the dorsum; fourth pair, if present, situated close to the anus. Deposits large primary crosses with central bipartite apophyses scattered on dorsum and ventrum. Rods present in tentacles, papillae and tube feet. Colour in alcohol dark violet

Distribution. This species is known from the Gulf of Mexico, Southern Indian Ocean, and Pacific Ocean (Rogacheva et al. 2009). The depth range is 3,294–4,301 m (Rogacheva et al. 2009). Probably a different species is distributed in the northeastern Atlantic, between 4,400–4,848 m (Pawson et al. 2015). The present record would be the first from the Colombian Caribbean Sea and the Caribbean.

Comments. Identification was made on the basis of external characteristics presented by Rogacheva et al. (2009), who redescribed the species and designated a lectotype, and *in situ* photographs by Pawson et al. (2015), who first recorded the species in the Gulf of Mexico. *Benthodytes lingua*, recorded in Colombia and the Caribbean Sea, differs from *B. abyssicola* by having 12 pairs of dorsal papillae throughout the two dorsal radii (Martinez et al. 2014), with some of them are larger (WoRMS 2019f), in comparison with those observed in the specimens recorded in the present study. Taxonomic characters in *Benthodytes* include number of tentacles, shape of the body wall deposits, and position of dorsal appendages, which are the most important diagnostic external characters, especially for the identification from images. Identification of *Benthodytes* species can be difficult, depending on the quality of the images and the angle from which individuals are observed. During this assessment, images were acquired of what were believed to correspond to three different species. However, all of them are presented as "cf.", as follows. Currently, *Benthodytes* includes 14 species (WoRMS 2019e). Of them, *B. lingua* Perrier R., 1896, *B. sanguinolenta* Théel, 1882, *B. typica* Théel, 1882, and *B. abyssicola* Théel, 1882 have been recorded at the Gulf of Mexico and the Caribbean Sea (Pawson et al. 2009, 2015; Alvarado and Solís-Marín 2013). Particularly for the Colombian Caribbean Sea, *B. sanguinolenta*, *B. typica*, and *B. lingua* are currently listed (Borrero-Pérez et al. 2012; Borrero-Pérez et

al. 2019).

***Benthodytes* cf. *sanguinolenta* Théel, 1882**
Figure 3M

Material examined. COLOMBIA • 1; Southwestern Caribbean, Gorgon A-1; 09.433°N, 076.748°W; depth 2307 m; 26 Apr. 2017; ROV, Moving Image; ACC: ROV-2017-Gorgon 1 final seabed survey 26 April 2017 37.51.

Identification (after Théel 1882; Rogacheva et al. 2009). Body elongated, more or less cylindrical, six to seven times longer than broad. Eighteen tentacles. Dorsal papillae many, very minute, retracted, often only dark-colored, water-vascular canals can be found. Dorsal papillae arranged in two bands with 1–4 papillae edgewise in a band, narrowing to 1 or 2 papillae edgewise in a band at the posterior end. Sometimes papillae present between the 2 bands. Immediately behind the gonopore, papillae are scattered irregularly, not forming bands. Integument thin and pliable, without ossicles. Colour in alcohol red, inclining to violet; the back lighter excepting its processes, which are of darker colour.

Distribution. Cosmopolitan species, recorded in the Colombian Caribbean Sea (Bayer et al. 1970; Borrero-Pérez et al. 2012); Atlantic Ocean (Mid-Atlantic Ridge, Peru Basin, near Bahama Islands, Gulf of Mexico and Caribbean Sea), Pacific (Tasman Sea, Kermadec Trench, off Panama isthmus, Japan and from the Cascadia basin), Indo-Pacific region, South Africa, the Bay of Bengal and Crozet Islands (Bayer et al. 1970; Rogacheva et al. 2009; Pawson et al. 2009; Borrero-Pérez et al. 2012). Depth range: 768–7250 m (Rogacheva et al. 2009).

***Benthodytes* cf. *typica* Théel, 1882**
Figure 3H–J

Material examined. COLOMBIA • 1; Southwestern Caribbean, Calasú 1; 10.471°N, 076.235°W; depth 2259 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L02:2276 • 1; Southwestern Caribbean, Calasú 1; 10.471°N, 076.235°W; depth 2257 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L02:2287 • 1; Southwestern Caribbean, Calasú 1; 10.471°N, 076.235°W; depth 2245 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L02:2295 • 1; Southwestern Caribbean, Calasú 1; 10.471°N, 076.235°W; depth 2309 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L02:2336 • 1; Southwestern Caribbean, Calasú 1; 10.493°N, 076.21°W; depth 2387 m; 29 Sep. 2015; towed camera, still image; ACC:TC-2015-L01:2401 • 1; Southwestern Caribbean, Calasú 1; 10.377°N, 076.31°W; depth 2226 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L12:2403 • 1; Southwestern Caribbean, A; 10.296°N, 076.461°W; depth 2488 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L13:2403 • 1; Southwestern Caribbean, Calasú 1; 10.38°N, 076.319°W; depth 2354 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L09:2414 • 1; Southwestern Caribbean, Calasú 1; 10.493°N, 076.21°W; depth 2377 m; 29 Sep. 2015; towed camera, still image; ACC:TC-2015-L01:2420 • 1; Southwestern Caribbean, A; 10.296°N, 076.461°W; depth 2486 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L13:2422 • 1; Southwestern Caribbean, A; 10.296°N, 076.461°W; depth 2486 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L13:2425 • 1; Southwestern Caribbean, Calasú 1; 10.493°N, 076.21°W; depth 2371 m; 29 Sep. 2015; towed camera, still image; ACC:TC-2015-L01:2428 • 1; Southwestern Caribbean, Calasú 1; 10.38°N, 076.319°W; depth 2355 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L09:2434 • 1; Southwestern Caribbean, A; 10.296°N, 076.461°W; depth 2484 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L13:2458 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 2077 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2465 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 2076 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2472 • 1; Southwestern Caribbean, Calasú 1; 10.467°N, 076.242°W; depth 2302 m; 30 Sep. 2015; towed camera, still image; ACC:TC-2015-L03:2508 • 1; Southwestern Caribbean, Calasú 1; 10.467°N, 076.242°W; depth 2303 m; 30 Sep. 2015; towed camera, still image; ACC:TC-2015-L03:2509 • 1; Southwestern Caribbean, Calasú 1; 10.467°N, 076.242°W; depth 2320 m; 30 Sep. 2015; towed camera, still image; ACC:TC-2015-L03:2527 • 1; Southwestern Caribbean, Calasú 1; 10.38°N, 076.319°W; depth 2353 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L09:2537 • 1; Southwestern Caribbean, Calasú 1; 10.467°N, 076.242°W; depth 2340 m; 30 Sep. 2015; towed camera, still image; ACC:TC-2015-L03:2551 • 1; Southwestern Caribbean, A; 10.296°N, 076.461°W; depth 2499 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L13:2553 • 1; Southwestern Caribbean, A; 10.281°N, 076.445°W; depth 2563 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L14:2587 • 1; Southwestern Caribbean, Calasú 1; 10.48°N, 076.224°W; depth 2339 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L04:2598 • 2; Southwestern Caribbean, Calasú 1; 10.48°N, 076.224°W; depth 2343 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L04:2602 • 1; Southwestern Caribbean, Calasú 1; 10.48°N, 076.224°W; depth 2340 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L04:2603 • 1; Southwestern Caribbean, Calasú 1; 10.48°N, 076.224°W; depth 2563 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L04:2604 • 1; Southwestern Caribbean, A; 10.281°N, 076.445°W; depth 2393 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L14:2649 • 1; Southwestern Caribbean, Calasú 1; 10.381°N, 076.326°W; depth 2565 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L10:2680 • 1; Southwestern Caribbean, A; 10.281°N, 076.445°W; depth 2381 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L14:2696 • 1; Southwestern Caribbean, Calasú 1; 10.381°N, 076.326°W; depth 2563 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L10:2749 • 1; Southwestern Caribbean, A; 10.281°N, 076.445°W;

depth 2374 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L14:2765 • 2; Southwestern Caribbean, A; 10.281°N, 076.445°W; depth 2563 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L14:2773 • 1; Southwestern Caribbean, A; 10.281°N, 076.445°W; depth 2294 m; 30 Sep. 2015; towed camera, still image; ACC:TC-2015-L14:2819 • 1; Southwestern Caribbean, A; 10.281°N, 076.445°W; depth 2294 m; 30 Sep. 2015; towed camera, still image; ACC:TC-2015-L14:2820 • 1; Southwestern Caribbean, Calasú 1; 10.381°N, 076.326°W; depth 2362 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L10:2828 • 1; Southwestern Caribbean, Calasú 1; 10.466°N, 076.242°W; depth 2297 m; 30 Sep. 2015; towed camera, still image; ACC:TC-2015-L05:2835 • 1; Southwestern Caribbean, Calasú 1; 10.381°N, 076.326°W; depth 2358 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L10:2843 • 1; Southwestern Caribbean, Calasú 1; 10.466°N, 076.242°W; depth 2304 m; 30 Sep. 2015; towed camera, still image; ACC:TC-2015-L05:2852 • 1; Southwestern Caribbean, Calasú 1; 10.381°N, 076.326°W; depth 2356 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L10:2860 • 1; Southwestern Caribbean, Calasú 1; 10.466°N, 076.242°W; depth 2308 m; 30 Sep. 2015; towed camera, still image; ACC:TC-2015-L05:2868 • 1; Southwestern Caribbean, Calasú 1; 10.466°N, 076.242°W; depth 2307 m; 30 Sep. 2015; towed camera, still image; ACC:TC-2015-L05:2869 • 1; Southwestern Caribbean, Calasú 1; 10.392°N, 076.325°W; depth 2426 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L11:2953 • 1; Southwestern Caribbean, Calasú 1; 10.392°N, 076.325°W; depth 2414 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L11 3061 • 1; Southwestern Caribbean, Calasú 1; 10.392°N, 076.325°W; depth 2411 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L11:3081 • 1; Southwestern Caribbean, Calasú 1; 10.469°N, 076.25°W; depth 2371 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L07:3275 • 1; Southwestern Caribbean, Calasú 1; 10.476°N, 076.247°W; depth 2403 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L08:3345.

Identification (after Théel 1882). Body more or less depressed, oval, from 1.5–2× as long as broad; its brim very broad. Twenty tentacles. Integument without papillae; about eight minute processes arranged along each of the dorsal ambulacra. Integument rather thick, soft, and transparent, with scattered more or less curved, unbranched and spinose calcareous. Colour in alcohol light bluish, the ventral surface blood-red or purple; the canals, which belong to the minute pedicels situated around the brim show the aspect of deep reddish bands which radiate towards the circumference of the body.

Distribution. *Benthodytes typica* is a well-known species from the Gulf of Mexico (Pawson et al. 2009; Pawson et al. 2015). In the Western Atlantic is also distributed in Martinique, Bequoia, west of Haiti, and from Cape Hatteras to Nantucket. It is also known from the eastern Atlantic, off the Azores; depth range 1,400–3,514 m (Deichmann 1930). It has been recorded in Colombia from the Seaflower Biosphere Reserve (Borrero-Pérez et al. 2019).

Comments. The present record is the second for the Colombian Caribbean Sea being the nearest to the Colombian continental coast. *Benthodytes* cf. *typica* was the most common species observed in the towed camera images during this research. One image showed a specimen of *B.* cf. *typica* swimming, a behavior that has been previously reported for juveniles (Billett et al. 1985). Rogacheva et al. (2012) reported other *Benthodytes*: *B. gosarsi* Gebruk, 2008 and *B. lingua* as occasional deep-sea holothurian swimmers, meaning that they swim rarely, usually in response to disturbance or when changing location at the seafloor.

Genus *Psychropotes* Théel, 1882

***Psychropotes depressa* (Théel, 1882)**
Figure 4A–E

Material examined. COLOMBIA • 1; Southwestern Caribbean, E; 9.011°N, 076.917°W; depth 1217 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L19:2399 • 1; Southwestern Caribbean, E; 9.011°N, 076.917°W; depth 1216 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L19:2405 • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 2090 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L16:2416 • 1; Southwestern Caribbean, E; 9.011°N, 076.917°W; depth 1182 m; 4 Oct. 2015; towed camera, still image; ACC:TC-2015-L19:2494 • 1; Southwestern Caribbean, Calasú 1; 10.38°N, 076.319°W; depth 2354 m; 1 Oct. 2015; towed camera, still image; ACC:TC-2015-L09:2503 • 2; Southwestern Caribbean, Calasú 1; 10.381°N, 076.326°W; depth 2398 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L10:2622 • 1; Southwestern Caribbean, A; 10.281°N, 076.445°W; depth 2566 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L14:2707 • 1; Southwestern Caribbean, A; 10.298°N, 076.449°W; depth 2528 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L15:2850 • 1; Southwestern Caribbean, Calasú 1; 10.392°N, 076.325°W; depth 2426 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L11:2984 • 1; Southwestern Caribbean, Calasú 1; 10.392°N, 076.325°W; depth 2421 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L11:3012 • 1; Southwestern Caribbean, Calasú 1; 10.392°N, 076.325°W; depth 2419 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L11:3038.

Identification (After Pawson et al. 2005; Hansen 1975; Deichmann 1930). Body flattened ventrally, arched dorsally, approximately twice as long as wide; ventrolateral brim around the entire body, conspicuously widening anteriorly. Ventral anus and mouth. Body wall translucent, intestine visible through the body wall near the posterior end, and dorsal longitudinal muscles visible

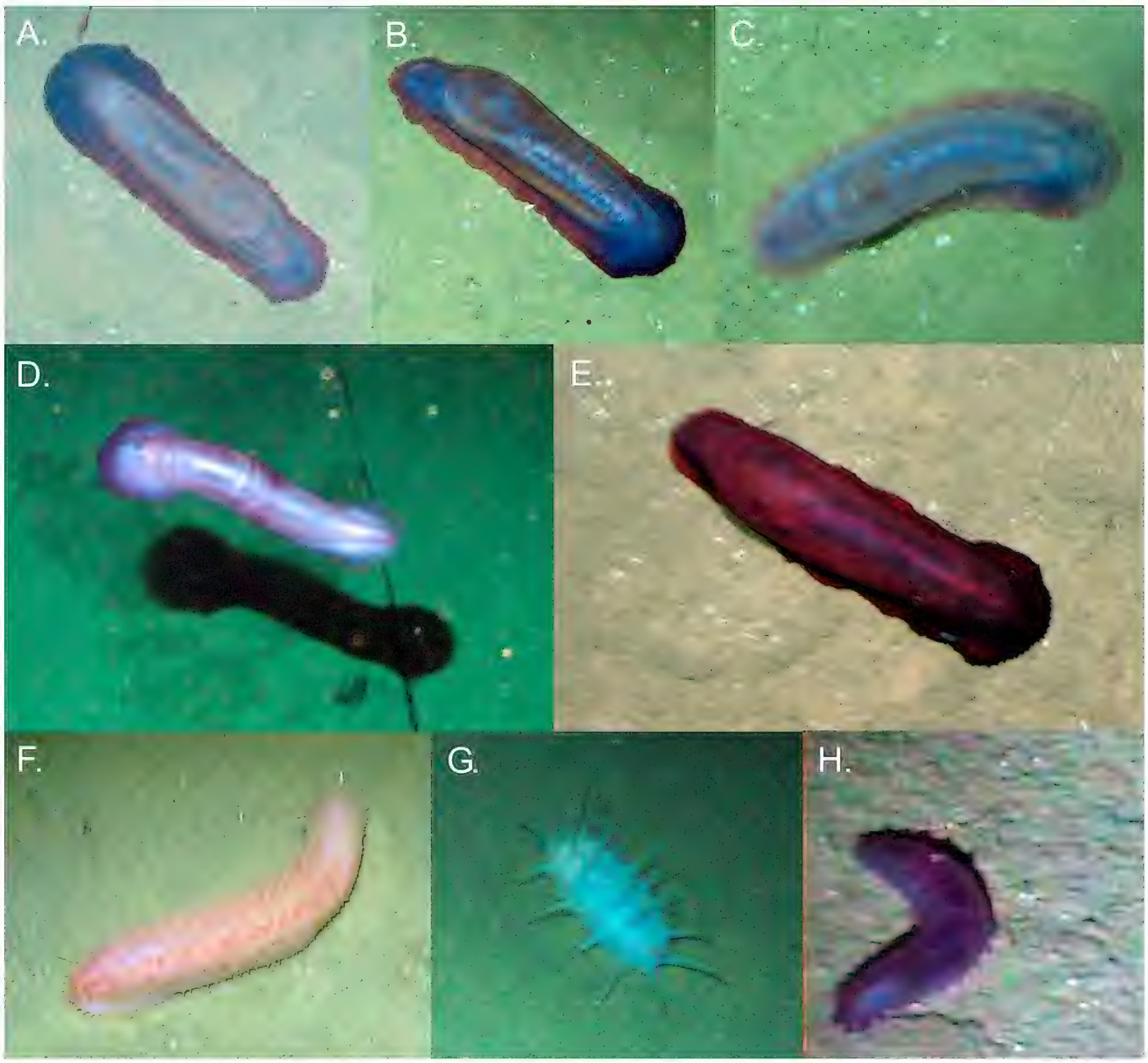

Figure 4. Towed-camera *in situ* images of deep-sea holothurians from the Colombian Southern Caribbean. **A–E.** *Psychropotes depressa*. **F.** ?*Synallactes* sp. **G.** *Deima validum validum*. **H.** *Laetmogone* sp. (ROV image).

along the entire body. Colour light violet, darker ventrally. A prominent dorsal projection as long as one-sixth of the body length and lies about one-third of the body length from the posterior end. This projection or appendage is a rudimentary veil that can be very variable in form and size. Three or more pairs of short and blunt projections are equally spaced along the inner edges of the dorsal radii, the posterior-most pair, placed at about mid-body, being the largest. The projections become smaller towards the anterior end. Eighteen tentacles

Distribution. Cosmopolitan; depth range 957–4,200 m (Rogacheva et al. 2013; Pawson et al. 2015). In the Western Atlantic, the species has been recorded in the Gulf of Mexico and Cuba (Alvarado and Solís-Marín 2013; Pawson et al. 2015). It has been recorded in Colombia from the Seaflower Biosphere Reserve (Borrero-Pérez et al. 2019).

Comments. The present record is the second for the Colombian Caribbean Sea and is the nearest to the Colombian continental coast. We identified the individuals from the Colombian Southern Caribbean as *P. depressa* on the basis of the diagnostic previously described external characters and the similarity of Colombian specimens with those identified in the Gulf of Mexico (Pawson et al. 2015). Rogacheva et al. (2012) recorded *P. depressa* as an occasional swimmer, usually in response to disturbance or when changing its location at the seafloor. We recorded at least three images of specimens swimming. One specimen observed in a darker purple colour may belong to a different *Psychropotes* species (Fig. 4E).

Order Synallactida Miller, Kerr, Paulay, Reich, Wilson, Carvajal & Rouse, 2017
Family Synallactidae Ludwig, 1894
Genus *Synallactes* Ludwig, 1894

? *Synallactes* sp.
Figure 4F

Material examined. COLOMBIA • 1; Southwestern Caribbean, B; 9.23°N, 076.571°W; depth 651 m; 5 Oct.

2015; towed camera, still image; ACC:TC-2015-L24:2476.

Comments. The specimen observed in the Colombian Southern Caribbean perhaps belongs to the genus *Synallactes*. The body is more or less cylindrical, flattened ventrally at the posterior end with a brim. Anus terminal, just above the brim. Pointed and slender dorsal papillae evenly distributed, although two dorsal-lateral rows are barely noted. Papillae at the anterior body end are in lower density, however with a large, irregular sized fringe of papillae. Colour in life is light pink. Currently, 26 species are recognized in the genus *Synallactes* (WoRMS 2019g), but only *S. crucifera* Perrier R., 1898 has been recorded from the Caribbean Sea (Alvarado and Solís-Marín 2013). There is no *Synallactes* species recorded in the Gulf of Mexico (Pawson et al. 2009; Pawson et al. 2015).

Synallactidae sp.
Figure 3N

Material examined. COLOMBIA • 1; Southwestern Caribbean, Calasú 1; 10.377°N, 076.31°W; depth 2236 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L12:2479. COLOMBIA • 1; Southwestern Caribbean, Calasú 1; 10.48°N, 076.224°W; depth 2348 m; 2 Oct. 2015; towed camera, still image; ACC:TC-2015-L04:2623. COLOMBIA • 1; Southwestern Caribbean, A; 10.281°N, 076.445°W; depth 2564 m; 3 Oct. 2015; towed camera, still image; ACC:TC-2015-L14 2657.

Comments. The three observed specimens are characterized by having the anterior end widened with a broad and darker colour brim, however the brim is not present at the posterior part of the body, which is tapered. Colour is dark purple, dorsal side surface looks smooth with apparent darker colored spots. The specimens observed in the Colombian Southern Caribbean Sea are similar to Synallactidae gen. et sp. indet. described and illustrated by Rogacheva et al. (2013: fig. 4A, B. 18C), which is currently without a name. The description presented by these authors, based on images and collected specimens, is detailed and includes ossicle information. For lower identification of the specimens reported in the present paper, more images and collected specimens are required. Puentes et al. (2019b) listed this morphotype as "*Benthodytes* sp.".

Family Deimatidae Théel, 1882
Genus *Deima* Théel, 1879

***Deima validum validum* Théel, 1879**
Figure 4G

Material examined. COLOMBIA • 1; Southwestern Caribbean, Kronos 1; 09.284°N, 076.776°W; depth 1986 m; 3 Oct. 2015; towed camera, still image; ACC: TC-2015-L16:2620.

Identification (after Deichmann 1930). Short forms; tentacles small, retractile, lateral feet in simple rows; dorsal papillae also in simple rows.

Distribution. Cosmopolitan species, occurring from tropical to moderate latitudes; depths range 724–5424 m (Rogacheva et al. 2013). In the Western Atlantic, the species has been recorded in the Gulf of Mexico, Cuba, Venezuela, and Brazil (Alvarado and Solís-Marín 2013). In Colombia it has been recorded from the oceanic area in the Seaflower Biosphere Reserve (Borrero-Pérez et al. 2019).

Comments. *Oneirophanta* Théel, 1879 is distinguished from *Deima* by the elongate form, large non-retractile tentacles, lateral feet arranged in a zigzag row, and dorsal papillae in simple or double rows. The present record is the second for the Colombian Caribbean Sea and the nearest to the Colombian continental coast. Currently, one species with two subspecies are recognized in the genus *Deima*: *D. validum validum* Théel, 1879 and *D. validum pacificum* Ludwig, 1894 (WoRMS 2019h). This last subspecies has few records, only in the Eastern Pacific and Indo-Pacific (*D. validum* subsp. *pacificum*; GBIF 2017).

Discussion

Interest in hydrocarbon resource exploration of the bathyal and abyssal plains in the Colombian Caribbean has increased substantially in the last years. Exploratory activities associated with this resource, and in support of its sustainable use, have generated key biological information that is paramount for the characterization of these unknown and remote areas. Among the deep-sea fauna, holothurians dominate the abyssal benthic communities, and they can make up to 90% of the ecosystem biomass (Hendler et al. 1995; FitzGeorge-Balfour et al. 2010). Deep-sea cucumbers, mostly deposit-feeders, are key consumers and sediment bioturbators that modify the quality of organic matter in the sediment and process fresh phytodetritus and minerals through nutrient regeneration and respiration (Smallwood et al. 1999; Bett et al. 2001; FitzGeorge-Balfour et al. 2010; Thurber et al. 2014). Considering their involvement in these key functions of deep-sea ecosystems, holothurians have been used to evaluate the recovery of population density, community composition, and respiration activity after deep-sea disturbance experiments (Stratmann et al. 2018).

The North Atlantic is one of the best-explored regions of the deep ocean; about 55 holothurian species are known (Rogacheva et al. 2013). In Latin American countries, including the Caribbean Sea and the South Atlantic, fewer studies at depths below 1,000 m have reported a total of 34 sea cucumber species, 16 of which are present in the Colombian Caribbean (Pérez-Ruzafa et al. 2013; Benavides-Serrato et al. 2013). In the Gulf of Mexico, the most complete inventory of echinoderms catalogued 23 deep-sea cucumber species (Pawson et al. 2009); recently, approximately 10 holothurian species

were recorded by the first time in the Gulf of Mexico (Pawson et al. 2015). Based on good-quality images, the present study reveals that deep-sea environments in the Colombian Southern Caribbean Sea hold a higher number of species than what was known. In addition, taxa that were identified to the family or genus level might represent new records or even new species.

In Colombia, previous deep-sea holothurian research has been done down to a depth of 1000 m using benthic trawls (Borrero-Pérez et al. 2003; Benavides-Serrato and Borrero-Pérez 2010). Images and videos obtained in our study using ROV and towed camera systems allowed us to explore deeper and different environments, assessing habitats where trawling is challenging. In addition, *in situ* observations using these technologies provide not only behavioral, biological, and ecological information, but also specific data on the external live appearance of animals that are easily damaged by conventional sampling methods, as deep-sea cucumber specimens are usually fragile and/or gelatinous (Rogacheva et al. 2013). However, in spite of the knowledge of these important external characters, most deep-sea holothurians cannot be identified to species or even genera by photographs alone due to the need to observe ossicle morphology, which is the main taxonomic character in sea cucumbers. Several studies have demonstrated that more significant information on deep-sea holothurians is obtained by combining data from trawl catches with observations and sampling from ROV video surveys (Rogacheva et al. 2013).

ROV and towed camera images and videos from the Colombian Southern Caribbean Sea allowed us to recognize species of holothurians that had not been collected by trawling, and we are presenting several new records for the Caribbean Sea and even the Atlantic Ocean. Although some identifications are yet to be confirmed, these technologies and the information that they provide are valuable for initiating and/or increasing the knowledge of the deep-sea cucumbers in unexplored areas. It is clear that for some groups, such as the genus *Benthodytes,* specimens are required to confirm species identifications. However, on the basis of the present results we already know that it is one of the most species-rich genera. Qualitative field studies like ours can potentially provide the baseline data to increase the knowledge of these ecosystems. Still, more detailed taxonomic and ecological research, based on a combined strategy allowing both imaging and sampling of specimens, is necessary for confirmation of some species, to increase the biodiversity inventories, and to understand the functioning of these environments.

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